

## NESTING SUCCESS AND PRODUCTIVITY OF HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

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ABSTRACT.—Predation was the major source of nest failure for hummingbirds studied in southwestern New Mexico and southeastern Arizona, accounting for nearly 80% of all failed nest attempts. Predation on eggs was responsible for just over 70% of all losses attributed to predation; predation on nestlings accounted for <30% of the losses. Nest failures resulting from abandonment, structural failure, and infertility were low and similar to that found in other studies dealing with altricial young. On an annual basis, nesting success ranged from 0% for Costa's Hummingbirds (*Calypte costae*) in 1976 and 1980, to 80% for Broad-billed Hummingbirds (*Cynanthus latirostris*) in 1977. Significant differences in egg and nestling survival between early and late nests were found for Black-chinned Hummingbirds (*Archilochus alexandri*) in one of the three study areas. Average productivity (number of young fledged per female), based on data from all years and each study area, ranged from  $0.16 \pm 0.27$  [SD] young per female for Costa's Hummingbirds to  $2.32 \pm 0.08$  for Broad-billed Hummingbirds. Productivity for Black-chinned Hummingbirds, the most numerous of the five species studied, averaged  $1.16 \pm 0.87$ , while that of Violet-crowned Hummingbirds (*Amazilia violiceps*) averaged  $1.43 \pm 0.02$ . Productivity for Magnificent Hummingbirds (*Eugenes fulgens*), which nested only during 1976, was 1.16 young per female. Results of the present study are consistent with those of previous studies that have dealt with nesting female hummingbirds, and suggest that predation and productivity are more generalized than might be expected based on the range of habitats occupied. Received 22 July 1985, accepted 29 Jan. 1986.

Most studies of hummingbirds have concentrated on males or on the coevolution of plant pollinator systems, optimal foraging and energetics, territoriality, or on the organization of tropical communities. The few studies that have examined the ecology of nesting female hummingbirds in detail include those by Pitelka (1951a, b), Legg and Pitelka (1956), Calder (1973), Stiles (1973), Carpenter (1976), and Calder et al. (1983).

This paper presents the findings of a portion of a larger study (Baltosser 1978, 1983) that focused on the nesting ecology of female hummingbirds in southwestern New Mexico and southeastern Arizona. Here I (1) discuss the relative importance of predation and other sources of nest failure in terms of how they affected the nesting success and productivity of Black-chinned (*Archilochus alexandri*), Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), Costa's (*Calypte costae*), and Magnif-

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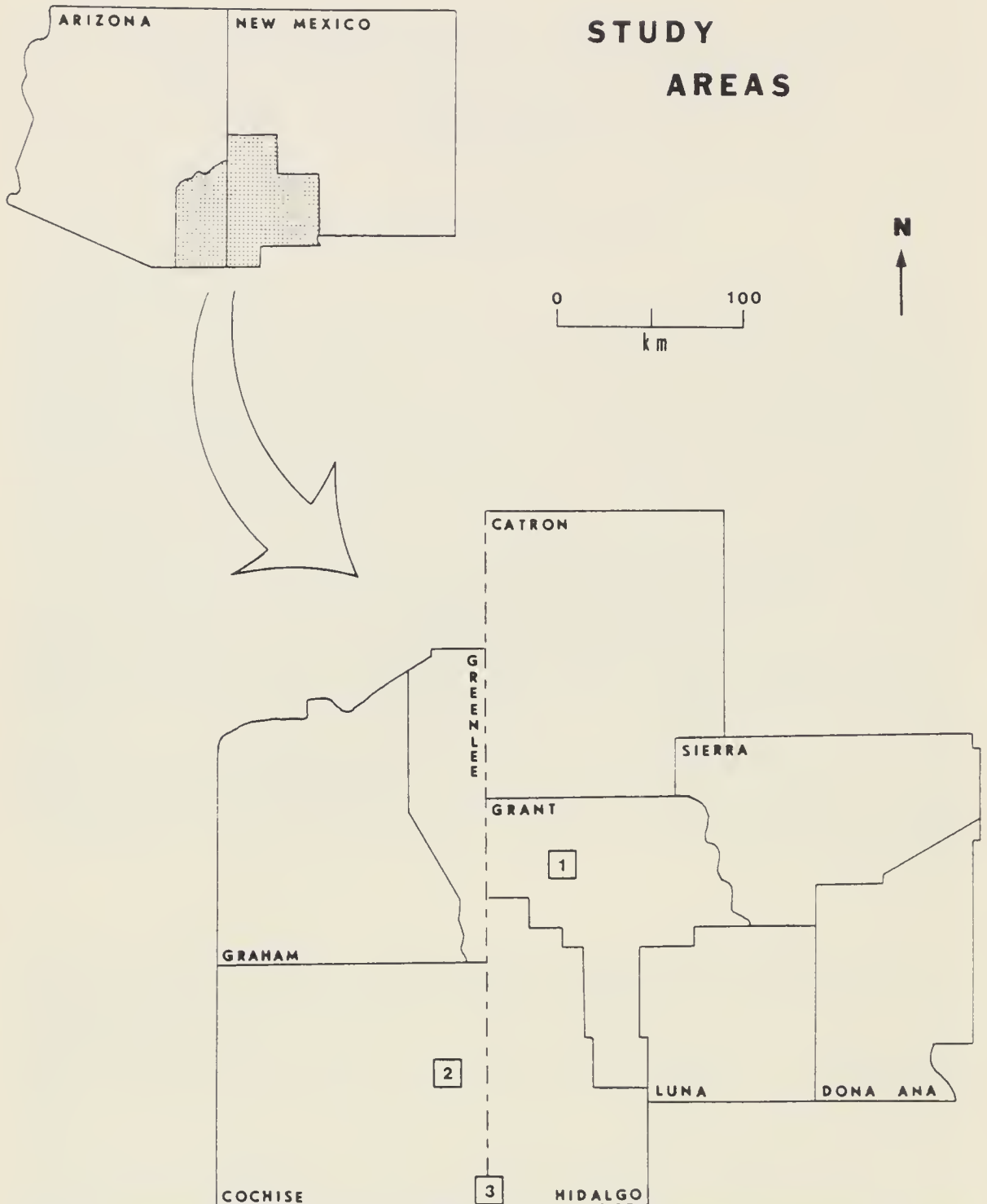


FIG. 1. Locations of the Cliff (1), Rucker Canyon (2), and Guadalupe Canyon (3) study areas.

icent (*Eugenes fulgens*) hummingbirds and (2) compare nesting success in these species with that of other temperate and tropical hummingbird species. With the exception of productivity values reported for Broad-tailed Hummingbirds (*Selasphorus platycercus*) by Waser and Inouye (1977) and Calder et al. (1983), the values presented in the present study are among the first reported for hummingbirds.

## STUDY AREAS

*Cliff*.—The area (elevation 1370 m) is near the town of Cliff along the east bank of the Gila River in Grant County, New Mexico (Fig. 1). It is approximately 990 m long and 42–104 m wide (9 ha), and is one of the longest continuous stands of woodland along the river. Numerous box-elder (*Acer negundo*), Goodding willow (*Salix gooddingii*), and Fremont cottonwood (*Populus fremontii*) trees characterize the upper story. The understory consists of woody and herbaceous species that include seepwillow (*Baccharis glutinosa*), skunk-bush (*Rhus trilobata*), chuchapate (*Ligusticum porteri*), buffaloweed (*Ambrosia trifida*), and various species of grass. Adjacent habitats include abandoned farm land, farmed land, and habitats similar to that of the study area.

*Rucker Canyon*.—The area (elevation 1870 m) is on the west side of the Chiricahua Mountains in Cochise County, Arizona (Fig. 1). It is confined primarily to an 800 × 75 m (5 ha) portion of the wooded creek bottom. Trees found within the area include several species of oak (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), Arizona cypress (*Cupressus arizonica*), pines (*Pinus ponderosa* and *P. chihuahuana*), and Arizona sycamore (*Platanus wrightii*). The understory includes wild bean (*Phaseolus grayanus*), skunk-bush, and various species of grass. Adjacent hillsides are vegetated with oak and juniper interspersed with open areas containing numerous agaves (*Agave parryi*).

*Guadalupe Canyon*.—The area is along the United States-Mexico border in extreme southwestern New Mexico and extreme southeastern Arizona (Fig. 1). From its source in the Peloncillo Mountains of New Mexico, the canyon drains to the southwest, passing through Arizona before entering Mexico. Within Mexico the canyon joins the Río de San Bernardino, a tributary of the Río Yaqui. The area of study was confined primarily to the 150-m-wide canyon bottom that rises from the International Boundary northeastward into the New Mexico portion of the canyon, a distance of 8500 m (total area approximately 106 ha). The elevation of the canyon bottom ranges from 1305 m in the Arizona portion to 1366 m in the New Mexico segment.

Guadalupe Canyon is surrounded by Chihuahuan Desert scrub vegetation that interdigitates with the riparian vegetation of the creek bottom. On the basis of topography, exposure, and vegetation, I recognized three major habitats: riparian creek bottom, precipitous north-facing slopes, and xeric south-facing slopes. The creek bottom is characterized by numerous open areas interspersed with clumps of mature Arizona sycamores and Fremont cottonwoods, with understories of seepwillow and burro-brush (*Hymenoclea monogyra*) in central portions, and honey mesquite (*Prosopis glandulosa*), red barberry (*Berberis haematocarpa*), and netleaf hackberry (*Celtis reticulata*) near the edges. North-facing slopes generally rise abruptly from the canyon floor and are characterized by open areas interspersed with netleaf hackberry, one-seed juniper (*Juniperus monosperma*), oaks (*Quercus arizonica* and *Q. grisea*), soapberry (*Sapindus saponaria*), and agaves (*Agave schottii* and *A. parryi*), with dense shrub thickets composed of red barberry, honey mesquite, gray-thorn (*Condalia lyciodes*), woolly buckthorn (*Bumelia lanuginosa*), and poison ivy (*Rhus radicans*). Most south-facing slopes rise gradually from the canyon bottom and are characterized by open areas with scattered agaves and ocotillo (*Fouquieria splendens*) or thickets of mixed species that include honey mesquite, little-leaf sumac (*Rhus microphylla*), and white-thorn (*Acacia constricta*).

## METHODS

*Locating nests*.—The majority of nests were found by walking the length of each study area several times at the onset of each nesting period. Additional nests were found incidentally during the course of study and by deliberate search in segments where no nests had previously been found. Based on subsequent searches that occurred every 7–10 days through-

out the nesting season, and the relatively few additional nests that were discovered, I estimate that 90–95% of all hummingbird nests were found.

*Loss assessment.*—Over 85% (176 nests) of the 206 nests used in this analysis were found while they were under construction or were in the early stages of incubation. Several nests of each species in each study area were selected for intensive study (56 nests total); the status of all remaining nests was nonetheless checked at least once every 7–10 days. The status of some nests was obtained directly because eggs or young could be seen. For most nests, however, several factors were used to assess their status. The attentive patterns of females and their behavior at the nest proved to be the best indicators of status for those nests whose eggs or young could not be seen. Nests known to have been completed during the current season, but for which no behavioral data were available, were occasionally found. In these few instances (13.6% of all nests), one or more subtle cues such as the size and shape of the nest (see Calder 1973), the presence of excrement adhering to foliage adjacent to the nest (indicative of large young and successful fledging), or the presence of eggshell fragments (indicative of eggs and subsequent predation) were used to deduce the probable outcome.

*Data analysis and presentation.*—Comparisons designed to test whether nesting success varied seasonally (i.e., early vs late nests) for Black-chinned and Broad-billed hummingbirds in Guadalupe Canyon were made. Comparisons were based on the number of nests that succeeded and failed, and they were analyzed using a *G*-test, which was adjusted using Williams' correction factor (Sokal and Rohlf 1981:736). Comparisons over the 3-year period for both species were analyzed by combining probabilities from the former calculations (Sokal and Rohlf 1981:780) and by inverse interpolation (Rohlf and Sokal 1981:xii).

Nesting success and productivity were calculated using methods described by Ricklefs (1969, 1973) and Ricklefs and Bloom (1977). Annual production (*P*) of fledglings by a female was calculated using the equation  $P = FB$ , where *F* is the expected rate at which young are fledged in a large population (young fledged/female × day) and *B* is the length of the breeding season (days).

The rate at which young are fledged (*F*) was calculated by the expression  $F = CSI$ , where *C* is clutch size, *S* is breeding success (proportion of individuals that fledge), and *I* is the rate of nest initiation (clutches/female × day). Rate of nest initiation was calculated by an equation that takes into account rate of nest failure and the interval between nestings, as follows (Ricklefs 1970):

$$I = \frac{m}{p_f + m(p_s r_s + p_f r_f)}$$

where *m* is equal to nest mortality rate (proportion of nests failing per day), *p<sub>s</sub>* is the probability that a nest successfully fledges at least one young, *p<sub>f</sub>* is the probability of a nest failing before fledging young ( $p_f = 1 - p_s$ ), *r<sub>s</sub>* is the delay before a new clutch is laid after successful fledging, and *r<sub>f</sub>* is the delay before a new clutch is laid after nest failure (*r<sub>s</sub>* and *r<sub>f</sub>* in the present study both = 10 days). Nesting success (*p<sub>s</sub>*) is related to daily mortality rate (*m*) by the following expression:

$$p_s = e^{-mT}$$

where *e* is the base of the logarithm and *T* is equal to the length of the nest cycle from the initiation of nesting until fledging (days).

Breeding season length was calculated from the number of nests initiated each month by the following equation:

$$B = 30 \exp(-\sum p_i \log_e p_i)$$

an index first used in the present context by MacArthur (1964). In this equation, *e* is the

base of the natural logarithm and  $p_i$  equals the proportion of clutches laid by a population during month  $i$ . This expression for breeding season takes into account the fact that breeding was not equally intense in all months during which eggs were found. The number of months of clutch initiation was multiplied by 30 to give the number of days ( $B$ ) during which clutches were initiated.

## RESULTS

*Predation and other sources of nest mortality.*—I found predation to be the major cause of nest failure. Of the 206 nests analyzed, 129 (79.1%) failed prior to fledging young (Table 1). Predation was responsible for 102 of the failed nest attempts. Egg predation accounted for 72.5% of all predation losses. Predation on nestlings accounted for the remaining 27.5%. Failures resulting from other sources accounted for only 20.9% of all failed nest attempts.

Proportions of all losses in different study areas resulting from predation were similar: 70.6% at Cliff, where only Black-chinned Hummingbirds nested; 68.0% at Rucker Canyon, where Black-chinned and Magnificent hummingbirds nested; and 83.9% in Guadalupe Canyon, where Black-chinned, Broad-billed, Violet-crowned, and Costa's hummingbirds nested. Predation rates of Black-chinned nests were similar in all areas: 70.6% of all losses at Cliff, 70.8% at Rucker Canyon, and 82.3% in Guadalupe Canyon. Predation accounted for 75.0% of all Broad-billed losses, 100% of all losses for Costa's, and 85.7% of all losses for Violet-crowned hummingbirds.

Predation rates varied seasonally for Black-chinned Hummingbirds in Guadalupe Canyon. Nectar resource abundance in this area was decidedly bimodal (Fig. 2). Hummingbird nesting results for this area, which also showed some degree of bimodality (Fig. 2), were thus segregated into two periods based on the differential availability and dispersion of nectar (Baltosser 1983). The first period included those nests initiated prior to the sharp decline occurring on or about 17 June and those of the second period were begun after this date in 1976, 1977, and 1980. Predation accounted for 88.9%, 100%, and 100% of all Black-chinned losses during the first period, and for 90.9%, 64.3%, and 75.0% of all losses during the second period. Predation rates between periods were not compared for Broad-billed Hummingbirds because of small sample size. Comparisons of predation rates between periods for Costa's and Violet-crowned hummingbirds were not possible because each nested only during one of the two periods. Costa's Hummingbird nesting was completed each year prior to the beginning of the second nesting period (i.e., before 17 June), and Violet-crowned Hummingbird nesting did not begin until the second nesting period was under way (i.e., after 17 June).

The death of well-developed nestlings in three nests in Rucker Canyon

TABLE 1  
 SOURCES OF NEST MORTALITY FOR BLACK-CHINNED (BC), MAGNIFICENT (MA),  
 BROAD-BILLED (BB), COSTA'S (CO), AND VIOLET-CROWNED (VC) HUMMINGBIRDS IN  
 SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

Sources of nest mortality	Species and area						
	BC <sup>a</sup>	BC <sup>b</sup>	MA <sup>b</sup>	BC <sup>c</sup>	BB <sup>c</sup>	CO <sup>c</sup>	VC <sup>c</sup>
Number of nests:							
Abandoned before eggs	3 (12) <sup>d</sup>	2 (7)	1 (50)	7 (7)	1 (5)	0	0
Egg mortality							
Egg predation	9 (35)	14 (47)	0	32 (32)	5 (25)	9 (82)	5 (31)
Structural failure	0	1 (3)	0	1 (1)	0	0	0
Eggs unhatched	0	0	0	1 (1)	1 (5)	0	0
Human intervention	0	1 (3)	0	0	0	0	0
Nestling mortality							
Nestling predation	3 (12)	3 (10)	0	19 (19)	1 (5)	1 (9)	1 (6)
Structural failure	0	0	0	1 (1)	0	0	0
Nestlings dead in nest	2 (8)	3 (10)	0	1 (1)	0	0	1 (6)

<sup>a</sup> Cliff study area.

<sup>b</sup> Rucker Canyon study area.

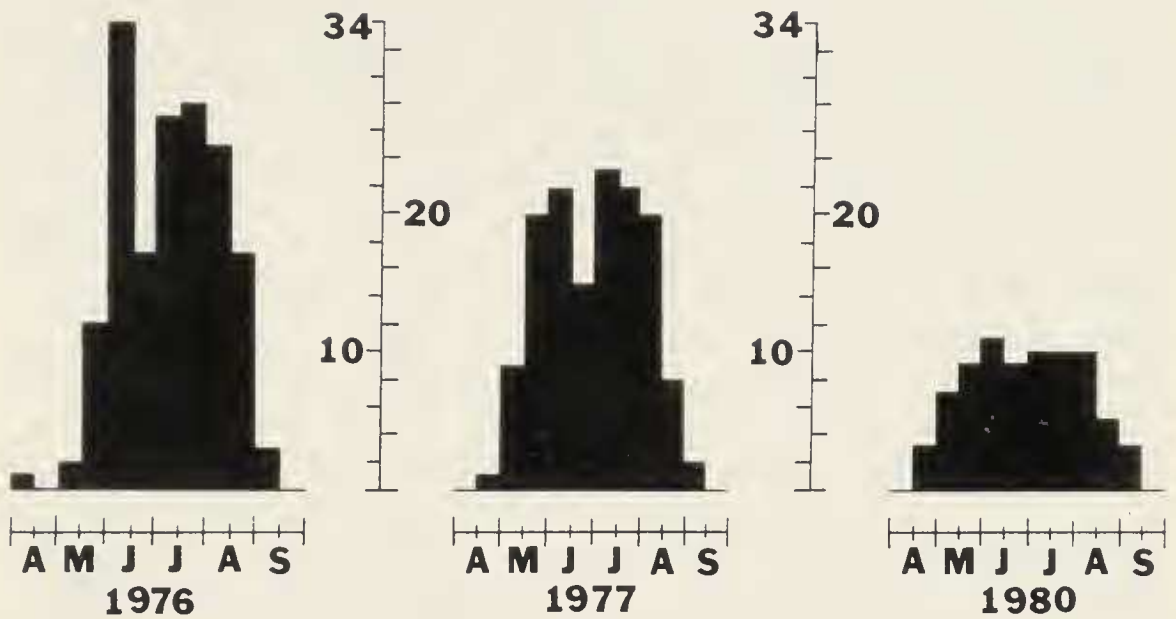
<sup>c</sup> Guadalupe Canyon study area.

<sup>d</sup> (Percent of all nests.)

in 1977 is believed to have resulted from inclement weather. During the 46-day period from 6 July through 20 August 1977, the study area received 22.3 cm of rain, which fell on 22 days. Only 6.93 cm of rain fell during the same period in 1976, and it rained on only 11 days. The presence of dead young that would have soon fledged in nests at Cliff may have also resulted from rainy weather, rather than from abandonment or mortality of the female. Indeed, a female at one of the two nests that contained dead nestlings built a second nest and initiated a new clutch on top of a large dead nestling that was sealed into the lower nest.

Daily mortality rates, which encompass all forms of nest failure, for all three areas and species nesting within these areas were just over 2.0% ( $\bar{x} = 2.28 \pm 1.22\%$  [SD]) of all nests in each population. Daily losses averaged  $2.52 \pm 0.15\%$  of all hummingbird nests at Cliff,  $3.10 \pm 1.56\%$  of all nests at Rucker Canyon, and  $1.99 \pm 1.20\%$  of all nests in Guadalupe Canyon. Pooled Black-chinned losses from each study area averaged  $3.01 \pm 1.01\%$  per day, while those of Broad-billed and Violet-crowned hummingbirds averaged  $1.22 \pm 0.86\%$  and  $1.36 \pm 0.25\%$ , respectively. Daily mortality, based on limited sample size, was 3.94% for Costa's Hummingbirds and 1.39% for Magnificent Hummingbirds.

**ACTIVE NESTS**



**1980 STANDING CROP (kj)**

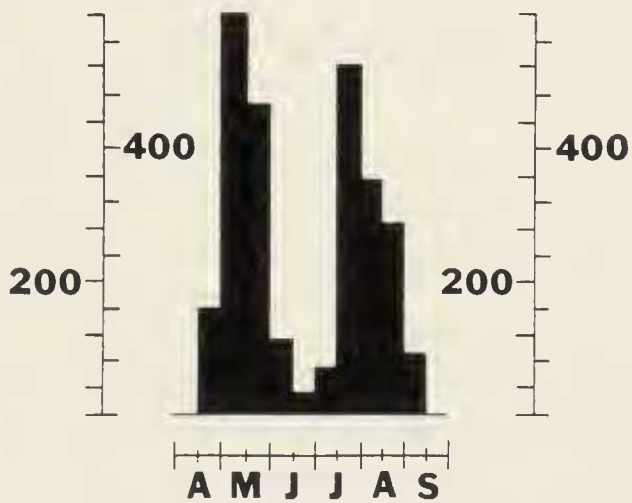


FIG. 2. Nesting phenology and abundance of active nests of hummingbird species in Guadalupe Canyon in relation to 1980 standing crop nectar values. (In 1976 and 1977 standing crops appeared to be similar to those of 1980, but only qualitative [i.e., abundance recorded as rare, common, or abundant] measurements were made.)

TABLE 2

YEARLY NESTING SUMMARY SHOWING THE TOTAL NUMBER OF BLACK-CHINNED, MAGNIFICENT, BROAD-BILLED, COSTA'S, AND VIOLET-CROWNED HUMMINGBIRD NESTS; THE NUMBER OF NESTS THAT PRODUCED FLEDGED YOUNG; AND THE PERCENT FLEDGING SUCCESS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

Species	Area	Year	No. nests	No. fledged (% fledging success)
Black-chinned	Cliff	1976	15	5 (33.3)
		1977	11	4 (36.4)
Black-chinned	Rucker Canyon	1976	17	4 (23.5)
		1977	13	2 (15.4)
Magnificent	Rucker Canyon	1976	2	1 (50.0)
		1977	0	0
Black-chinned	Guadalupe Canyon	1976	46	20 (43.5)
		1977	38	16 (42.1)
		1980	17	3 (17.7)
Broad-billed	Guadalupe Canyon	1976	10	6 (60.0)
		1977	5	4 (80.0)
		1980	5	2 (40.0)
Costa's	Guadalupe Canyon	1976	4	0
		1977	6	1 (16.7)
		1980	1	0
Violet-crowned	Guadalupe Canyon	1976	5	3 (60.0)
		1977	6	3 (50.0)
		1980	5	3 (60.0)

*Fledging success.*—I have defined fledging success as the proportion of nests, including those abandoned before eggs were laid, in which at least one young fledged. Average success for all species, areas, and years was  $37.0 \pm 22.4\%$  (Table 2). Success at Cliff was  $34.8 \pm 2.1\%$ , at Rucker Canyon  $29.6 \pm 18.1\%$ , and at Guadalupe Canyon  $39.2 \pm 25.5\%$ .

Black-chinned Hummingbird nesting success averaged  $19.5 \pm 5.8\%$  in Rucker Canyon and  $34.5 \pm 14.5\%$  in Guadalupe Canyon. Average success of Broad-billed Hummingbirds was  $60.0 \pm 20.0\%$ , that of Costa's  $5.6 \pm 9.6\%$ , and that of Violet-crowned Hummingbirds  $56.7 \pm 5.8\%$ .

Incubation success for Black-chinned Hummingbirds between the first and second nesting periods (Table 3) was not significantly different in 1976 ( $G_{adj} = 0.80$ ,  $df = 1$ ,  $P = 0.44$ ) or 1977 ( $G_{adj} = 2.90$ ,  $df = 1$ ,  $P = 0.09$ ). In the 1980 season, however, success during incubation was significantly greater in the second nesting period ( $G_{adj} = 5.56$ ,  $df = 1$ ,  $P =$



0.02). Incubation success for the cumulative three years between periods for this species was also significantly greater during the second nesting period ( $G_{\text{adj}} = 14.24$ ,  $df = 6$ ,  $P = 0.03$ ).

Black-chinned success during the nestling phase did not differ significantly between periods except for 1977, although in 1980 the difference approached significance ( $G_{\text{adj}} = 2.96$ ,  $df = 1$ ,  $P = 0.09$ ). Nestling success in 1977 was significantly greater during the first nesting period ( $G_{\text{adj}} = 6.08$ ,  $df = 1$ ,  $P = 0.02$ ).

Because greater incubation success during second nesting periods tended to be canceled by greater nestling success during first periods, overall success between periods for the duration of nesting did not differ significantly for Black-chinned Hummingbirds. Nesting success between periods, based on combined probabilities for all three years, also was not significantly different ( $G_{\text{adj}} = 2.78$ ,  $df = 6$ ,  $P = 0.83$ ).

Broad-billed Hummingbird incubation success between periods followed a pattern similar to that of Black-chinned Hummingbirds (Table 3). Success was greater during the second period except for 1977, but the seasonal differences were not significant. Only during 1980 did any of the values approach a level of significance ( $G_{\text{adj}} = 2.18$ ,  $df = 1$ ,  $P = 0.19$ ).

Broad-billed Hummingbirds were highly successful during the nestling phase, and only in 1980 did failures occur. Success for the duration of nesting between periods for Broad-bills was similar to that of Black-chins. Success was greater during the second period in 1976 and 1980 than in the first nesting period. Success in 1977 was, however, greater the first period than during the second period.

Comparisons of nesting success between periods within a given year for Costa's and Violet-crowned hummingbirds were not made because each nested only during one of the two periods (Table 3). Between-year comparisons of the same nesting periods for Costa's, however, did reveal some interesting trends. Nineteen seventy-seven was the only year the species had any success. Broad-billed success was greater during the first period in 1977, the only year in which that was the case. Nesting success of Violet-crowned Hummingbirds was similar between years.

*Productivity.*—Hummingbird productivity (number of young fledged per female), based on pooled data for each species, area, and year, was  $1.23 \pm 0.86$  young per female (Table 4). The average number of young produced per female was  $0.80 \pm 0.42$  at the Cliff study area,  $0.74 \pm 0.37$  at Rucker Canyon, and  $1.43 \pm 0.94$  at Guadalupe Canyon.

Black-chinned Hummingbird productivity in Guadalupe Canyon averaged  $1.82 \pm 0.99$ , as compared to  $0.80 \pm 0.05$  and  $0.53 \pm 0.05$  for the species at Cliff and Rucker Canyon, respectively. On a daily basis, Black-

TABLE 3  
 GUADALUPE CANYON HUMMINGBIRD NESTING SUMMARY FOR 1976, 1977, AND 1980  
 SHOWING THE PERCENT SURVIVAL OF NESTS (NESTING SUCCESS) FOR EACH SPECIES, STAGE,  
 AND PERIOD OF THE NESTING CYCLE

Species and stage of nesting	1976		1977		1980		All years	
	First nesting	Second nesting	First nesting	Second nesting	First nesting	Second nesting	First nesting	Second nesting
<b>Black-chinned</b>								
Incubation	68.0	80.0	42.9	70.6	16.7	80.0	48.3	76.2
Nestling	52.9	68.8	100	58.3	100	25.0	71.4	59.4
Overall	36.0	55.0	42.9	41.2	16.7	20.0	34.5	45.2
<b>Broad-billed</b>								
Incubation	50.0	71.4	100	66.7	33.3	100	57.1	75.0
Nestling	100	100	100	100	100	50.0	100	88.9
Overall	50.0	71.4	100	66.7	33.3	50.0	57.1	66.7
<b>Costa's</b>								
Incubation	0		33.3		0		18.2	
Nestling	0		50.0		0		50.0	
Overall	0		16.7		0		9.1	
<b>Violet-crowned</b>								
Incubation		80.0		66.7		60.0		68.8
Nestling		75.0		75.0		100		81.8
Overall		60.0		50.0		60.0		56.3

chinned Hummingbird productivity was 0.018 young per female in Guadalupe Canyon, 0.010 in Rucker Canyon, and 0.017 at Cliff.

Average productivity was  $2.32 \pm 0.08$  for Broad-billed Hummingbirds and  $1.43 \pm 0.02$  for Violet-crowned Hummingbirds. Costa's Hummingbirds rarely fledged young in Guadalupe Canyon, where their productivity was  $0.16 \pm 0.27$ . The productivity of Magnificent Hummingbirds at Rucker Canyon was 1.16 young per female. Daily productivity was virtually identical for Broad-billed (0.028 young/female) and Violet-crowned (0.027 young/female) hummingbirds, and greater than Costa's (0.003 young/female) and Magnificent (0.019 young/female) hummingbirds.

#### DISCUSSION

*Sources of mortality.* — Predation was the major cause of hummingbird nest failure in each of the three study areas. In other species of birds, mortality rates resulting from predation vary, but are frequently as low as 1/2%/day of all nests in a population in many large raptorial and oceanic species, and as high as 5%/day in some small land birds and precocial

TABLE 4  
 COMPONENTS OF BREEDING PRODUCTIVITY SHOWING THE NUMBER OF YOUNG FLEDGED PER FEMALE PER YEAR FOR BLACK-CHINNED,  
 MAGNIFICENT, BROAD-BILLED, COSTA'S, AND VIOLET-CROWNED HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN  
 ARIZONA

Species	Area	Year	Season length (months) <sup>a</sup>	Clutch size (eggs)	Nest mortality <sup>b</sup>	Nest period (days)	Nesting success <sup>c</sup>	Young/female
Black-chinned	Cliff	1976	1.10	2	0.0262	42	0.3333	0.50
		1977	1.99	2	0.0241	42	0.3636	1.10
Black-chinned	Rucker Canyon	1976	1.60	2	0.0344	42	0.2353	0.56
		1977	1.97	2	0.0446	42	0.1538	0.49
Magnificent	Rucker Canyon	1976	2.00	2	0.0139	50	0.5000	1.16
		1977	0	0	0	0	0	0
Black-chinned	Guadalupe Canyon	1976	3.23	2	0.0195	42	0.4400	2.11
		1977	4.09	2	0.0206	42	0.4210	2.63
		1980	3.44	2	0.0414	42	0.1760	0.72
Broad-billed	Guadalupe Canyon	1976	2.56	2	0.0096	42	0.6670	2.40
		1977	1.99	2	0.0053	42	0.8000	2.24
		1980	3.78	2	0.0218	42	0.4000	2.32
Costa's	Guadalupe Canyon	1976	1.75	2	0	45	0	0
		1977	1.89	2	0.0394	45	0.1667	0.47
		1980	1.00	2	0	45	0	0
Violet-crowned	Guadalupe Canyon	1976	1.65	2	0.0122	42	0.6000	1.44
		1977	1.96	2	0.0165	42	0.5000	1.40
		1980	1.65	2	0.0122	42	0.6000	1.44

<sup>a</sup> Number of months during which eggs were present.

<sup>b</sup> Proportion of nests in the population that failed each day.

<sup>c</sup> Proportion of nests that fledged at least one young.

species (Ricklefs 1969). Daily losses in my study averaged just over 2%. Failures resulting from other sources such as abandonment, structural failure, and infertility were of less importance and were similar to those found in other studies (see Ricklefs 1969).

I believe the majority of Black-chinned and Violet-crowned losses to predation in Guadalupe Canyon resulted from avian predators. This conclusion is based in part on the fact that I witnessed the loss of one Black-chinned nest to predation by Gray-breasted Jays (*Aphelocoma ultramarina*), on the frequent mobbing of Hooded Orioles (*Icterus cucullatus*) and Summer Tanagers (*Piranga rubra*), and on the fact that there was a significant inverse relationship ( $r = -0.65$ ,  $df = 11$ ,  $P < 0.05$ ) between nest height and nesting success for Black-chinned Hummingbirds (Baltosser 1983). Similarly, higher and more-exposed nests of Violet-crowned Hummingbirds, which were in microhabitats similar to Black-chinned Hummingbird nests (Baltosser 1983), also suffered greater predation.

Broad-billed Hummingbird losses to predation are thought to have resulted primarily from snake predation. Nests of this species were very close to the ground ( $\bar{x} = 1.1 \pm 0.5$  m), which placed them out of the path of most avian predators. The maximum diameter of limbs to which the pendent nests were attached was usually  $< 1$  cm, and predators other than snakes would have had difficulty extracting the contents without damaging the nest. With the exception of one nest that had a medium-sized hole similar to one a snake might produce when forcing eggs into its mouth, nests lost to predation were not altered and there were no eggshell fragments, which are often found in nests lost to avian predation.

Few data pertaining to possible sources of predation on Costa's Hummingbird nests were obtained because most nests were lost to predation very early in the nesting cycle. Few data that would indicate the source of predation on Black-chinned nests in Rucker Canyon and Cliff were obtained. Nests that failed were in some cases completely destroyed, while others were not appreciably altered.

*Nesting success and hummingbird productivity.*—Nesting success for hummingbird species in the present study, omitting Magnificent Hummingbirds because of extremely low sample size, was similar to that reported for other temperate and tropical hummingbirds (Woods 1927; Skutch 1931, 1940, 1966; Legg and Pitelka 1956; Stiles 1973; Carpenter 1976; Waser and Inouye 1977; Calder et al. 1983). Hummingbird nesting success in the above studies, based on 11 species and only those nests that contained eggs (i.e., nests abandoned before eggs were laid were not included) ranged from 20% to 89%. Average nesting success in the present study (deleting those nests abandoned before eggs were laid) ranged from

9% to 62%. Black-chinned nesting success for all three study areas was  $34.0 \pm 11.0\%$ , which is similar to the  $31.9 \pm 1.4\%$  reported for this species by Stiles (1973). Black-chinned success may therefore be relatively constant throughout the range of the species.

Nesting survivorship for all hummingbirds in each of the three study areas was generally higher during the nestling stage than during the incubation stage. This is consistent with other studies (see Best and Stauffer 1980) and probably stems in part from the fact that certain mortality factors, such as nest desertion, occur more frequently before hatching. In addition, especially vulnerable nests are more likely to be found and destroyed by predators early in the nesting cycle (e.g., Nolan 1978).

Ricklefs (1969) has suggested that in simpler habitats, or those with low productivity (i.e., arid and arctic), uncommon species tend to have relatively high nesting success as compared to more common species with similar nesting requirements. Reasons why rarer species like the Violet-crowned Hummingbird would experience greater success (56.7%) than more common species such as the Black-chinned Hummingbird (34.5%) were not given. During 1980, however, foliage in Guadalupe Canyon had been reduced by 75% as the result of an extremely severe freeze, and thus very little vegetative cover was available for nesting. Rarer and dominant Violet-crowned Hummingbirds nonetheless nested in virtually the same sites as in previous years, which were affected less by the freeze than sites available to Black-chinned Hummingbirds. The fewer Black-chinned Hummingbirds nesting in 1980 and their reduced nesting success in that year may have resulted in part from the effects of the freeze on vegetation. In contrast, in 1976 and 1977, poorer nesting success by Black-chinned Hummingbirds appeared to have been related to the amount of interference experienced by nesting female hummingbirds and subsequent predation resulting from the commotion and betrayal of the nest site (see Skutch 1949). In 1976, for example, there was a significant inverse correlation ( $r = -0.99$ ,  $df = 1$ ,  $P < 0.05$ ) based on 6663 minutes of intensive observation at 36 nests, between the number of times female Black-chinned, Broad-billed, and Violet-crowned Hummingbirds were disturbed or induced to leave their nests and their nesting success (Baltosser 1983). Similar interactions were frequently observed in 1977, but they were not quantified.

The exceptionally high nesting success (89%) of the Andean Hillstar (*Oreotrochilus estella*) reported by Carpenter (1976) is most likely related to the fact that it nests in enclosed and inaccessible rocky areas, including caves. Similarly, the greater nesting success of Broad-billed Hummingbirds (62%) in the present study was probably due in part to the protection

provided by their nest sites. Nests of this species were invariably next to rock outcrops or in extremely dense thickets, which provided a great deal of protection and seclusion.

In addition to predation, nesting success for Black-chinned Hummingbirds in Rucker Canyon and Cliff appeared to be affected by inclement weather. The death of well-developed nestlings in nests at Rucker Canyon and Cliff perhaps resulted from the dampness and cooler temperatures associated with extended periods of rainy weather.

Recently, Miller and Gass (1985) examined the available predation data on foraging adult hummingbirds in temperate habitats. They concluded that there is no indication that predation is a significant risk factor to adults. Much of my research (Baltosser 1978, 1983) supports their conclusions for foraging adults, but the results of the present study indicate that predation is an important mortality factor for hummingbird eggs and nestlings.

#### ACKNOWLEDGMENTS

I thank R. J. Raitt, P. W. Ewald, K. L. Bildstein, W. A. Calder, F. L. Carpenter, and T. L. Best for critically reviewing this manuscript. I thank R. S. Miller and C. L. Gass for sharing, prior to publication, their manuscript on survivorship in hummingbirds. I am indebted to the Magoffin and Hadley families of Guadalupe Canyon, the Hunt family at Cliff, and personnel of the Coronado National Forest at Rucker Canyon. Other individuals to whom I am extremely grateful include Mr. and Mrs. W. W. Baltosser, my wife Ginger, and my daughter Dianna. This work was supported in part by the New Mexico State University Department of Biology, the New Mexico Department of Game and Fish (contract no. 519-68-06), and Chapman Memorial grants (61462, 84472, and 110115) from the American Museum of Natural History.

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